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SEQUENTIAL CAVITY USE IN A COTTONWOOD BOTTOMLAND[1]

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Abstract. I studied the patterns and frequency of cavity reuse in a community of cavity-nesting birds in a cottonwood bottomland along the South Platte River in northeastern Colorado from 1985–1987. Of 100 cavities occupied in 1985, 56% were reused in 1986; 38.5% of 122 cavities occupied in 1986 were reused in 1987. Of 81 old cavities monitored in both 1986 and 1987, 65.4% were reused at least once. Similar proportions of secondary cavity-nesting bird (SCNB) and primary cavity-nesting bird (PCNB) cavities were reused in both years. Reoccupancy by the same species was 27% and 20.5% in 1986 and 1987, respectively, and was greater for SCNB than for PCNB cavities in both years. Conversely, reoccupancy by different species was greater for PCNB than for SCNB cavities in both years. Thus, old cavities of PCNB were more available to other species of cavity-nesting birds, whereas old SCNB cavities tended to be reused by the same species that previously occupied the cavity. SCNB used a greater proportion of old cavities than did PCNB in both 1986 and 1987. House Wrens (*Troglodytes aedon*) and Northern Flickers (*Colaptes auratus*) reoccupied most of the old cavities.

Key words: cavity-nesting birds, cavity reuse, sequential cavity use, Colorado, plains cottonwood, Populus sargentii.

INTRODUCTION

Most species of primary cavity-nesting birds (PCNB) excavate a new cavity each season (Short 1979, Thomas et al. 1979). Cavity excavation is an integral component of courtship in cavity-nesting birds (Lawrence 1967) and functions in pair bond formation and maintenance. In some species, each member of the pair may excavate a cavity each season, one of which will be used as the nesting cavity and the other as a roosting cavity or "emergency" cavity (Short 1979). New cavities may be excavated in spite of the existence of presumably suitable existing cavities because old, previously used cavities may contain parasites or debris that may make cavities less attractive (Moss and Camin 1970, Short 1979, Rendell and Verbeek 1996).

Because secondary cavity-nesting birds (SCNB) are unable to excavate cavities of their own, they depend on natural cavities created by wind damage or disease or on the excavation of cavities by PCNB. Although cavities are commonly used again and again by SCNB, the frequency of cavity reuse in a subsequent breeding season has been rarely addressed. Only two studies have examined cavity reuse: in these studies, constancy (= % reuse of the same holes in consecutive breeding attempts by the same species) ranged from 44% to 67% in a community of SCNB in Poland (Wesolowski 1989) and averaged 64.1% for ten SCNB in The Netherlands (Van Balen et al.1982).

Reuse of old cavities also occurs in PCNB, but apparently is relatively uncommon. Northern Flickers (*Colaptes auratus*) reuse old nest holes (Lawrence 1967, Gutzwiller and Anderson 1986, Ingold, pers. comm.), and Lawrence (1967) and Kilham (1962a) observed this in Yellow-bellied Sapsuckers (*Syphyrapicus varius*). Red-headed Woodpeckers (*Melanerpes erythrocephalus*) reuse abandoned Red-cockaded Woodpecker (*Dendrocopos borealis*) cavities (Baker 1971), and Ingold (1991) recorded two instances of Red-headed Woodpeckers returning to nest in the same cavities during consecutive seasons. Red-cockaded Woodpeckers commonly use the same nest cavities in successive years (Jackson 1978, 1987, Hooper et al. 1980), and Bent (1939) reported that Red-bellied Woodpeckers (*M. carolinus*) may occasionally reuse old cavities. In Acorn Woodpeckers (*M. formicivorus*), about half of the nests are in the same hole as previous nesting attempts (M. Stanback, pers. comm.). Wesolowski and Tomialojc (1986) described five cases of reoccupancy of old holes by *Dendrocopos major.* Although cavity reuse has been recorded for a number of species of PCNB, there is little information on the frequency with which it occurs.

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The frequency of cavity reuse likely depends on a number of factors, including the availability of old cavities and cavity substrates, the quality of cavities and surrounding habitats, the degree of nest-site fidelity (Ingold 1991), and competition for cavities by other cavity-nesting birds. An unusually high frequency of reuse by PCNB may suggest: (1) an inadequate substrate resource, (2) lowered excavation rates and, subsequently, fewer cavities available for SCNB (Kerpez and Smith 1990), (3) lowered reproductive output if older holes are less suitable in some way than new excavations, or (4) reduced fledgling survival if nesting is shifted to later in the season (Troetschler 1976) because PCNB are forced to reuse old cavities because of repeated losses of newly excavated cavities to competitors. Because nest sites are critical to reproductive success, patterns of cavity reoccupancy are central to understanding the population ecology and evolution of cavity-nesting birds, and may be useful in devising management strategies for cavity-nesters. This study details the use and reoccupancy of cavities for a community of cavity-nesting birds in a cottonwood bottomland.

METHODS

STUDY AREA

I studied sequential cavity use on the South Platte Wildlife Management Area (SPWMA) in a cottonwood bottomland along 30 km of the South Platte River near Crook, Logan County, Colorado. Elevations ranged from 1,116 to 1,149 m. Bottomland vegetation varied from 500 to 1,000 m wide and was bounded by uplands of sand sagebrush (*Artemisia filifolia*)-mixed prairie (Harrington 1954) and agricultural lands.

The riparian overstory was dominated by plains cottonwood (*Populus sargentii*) and peachleaf willow (*Salix amygdaloides*) (Sedgwick and Knopf 1986). Minor overstory components included boxelder maple (*Acer negundo*), Siberian elm (*Ulmus pumila*), and red ash (*Fraxinus pennsylvanica*). The understory shrub layer comprised primarily western snowberry (*Symphoricarpos occidentalis*), coyote willow (*Salix exigua*), sandbar willow (*S. interior*), poison ivy (*Toxicodendron radicans*), and Woods rose (*Rosa woodsii*), all of which generally occurred in discrete patches.

CAVITY USE

I searched for active cavities during April–June in 1985 and 1986. I found nests of 11 different species, including 5 primary excavators—Northern Flicker, Red-bellied Woodpecker, Red-headed Woodpecker, Downy Woodpecker (*Picoides pubescens*), and Black-capped Chickadee (*Parus atricapillus*), and 6 secondary cavity nesters—Wood Duck (*Aix sponsa*), American Kestrel (*Falco sparverius*), Great-crested Flycatcher (*Myiarchus crinitus*), White-breasted Nuthatch (*Sitta carolinensis*), House Wren (*Troglodytes aedon*), and European Starling (*Sturnus vulgaris*). Adults feeding young, excavating cavities, or frequently entering cavities were considered evidence of active nest sites. I checked cavities throughout the nesting season to verify that they were active. To relocate cavities in subsequent years, I marked nest trees with aluminum forester's tags, recorded tree distance and direction from permanently established steel "T-post" stakes, recorded orientation and height of cavities, and drew illustrations of that portion of the tree containing a cavity or cavities. To document cavity reuse, a subset of the nest sites located in 1985 and 1986 (i.e., cavities still intact and usable) was observed in 1986 and 1987 for up to three, 30-min intervals/nest site. Unusable cavities included those that had deteriorated (large, decayed openings in the walls of the cavity compartment) or resealed (see Sedgwick and Knopf 1991) or those that were unusable because the tree or limb containing the cavity had fallen.

Observations were distributed from mid-May through late June, the interval of primary cavity selection and hole occupancy. I recorded cavity reuse as (1) unused nest: no evidence of adult activity during any of three observation periods, and (2) used nest: multiple visits to the cavity by one or both adults, adult(s) feeding young, adult flushed from cavity by tapping tree, or nestlings heard in nest cavity. Two-tailed *t*-tests for proportions were used to test the significance of differences between percentages (Sokal and Rohlf 1969). Null hypotheses were rejected at $P = 0.05$.

RESULTS

CAVITIES REUSED

Of 100 active cavities originally located in 1985 and checked for reuse in 1986, 56% were reused: 54 cavities were reused by birds and 2 were reused by fox squirrels (*Sciurus niger*) (Table 1). A similar proportion of SCNB (53.1%) and PCNB (58.8%) cavities were reused (t_{98} =

TABLE 1. Cavity reuse, SPWMA, Colorado.

Original occupant	% reuse in 1986 of cavities located in 1985				% reuse in 1987 of cavities located in 1985–1986				% reuse in 1986–1987 of cavities located in 1985			
	Reuse	Constancy[a]	Usability[b]	Total *n*	Reuse	Constancy	Usability	Total *n*	Reused 1 year	Reused 2 years	Not reused	Total *n*
SCNB												
American Kestrel	66.7	44.4	22.2	9	41.7	25.0	16.7	12	25.0	50.0	25.0	8
European Starling	47.6	19.0	28.6	21	36.4	13.6	22.7	22	41.2	23.5	35.3	17
House Wren	62.5	56.3	6.3	16	57.1	57.1	0.0	14	25.0	41.7	33.3	12
White-breasted Nuthatch	0.0	0.0	0.0	3	33.3	33.3	0.0	3	0.0	0.0	100.0	1
Total	53.1	34.7	18.4	49	43.1	29.4	13.7	51	31.6	34.2	34.2	38
PCNB												
Northern Flicker	52.2	26.1	26.1[c]	23	33.3	24.2	9.1	33	31.8	22.7	45.5	22
Red-headed Woodpecker	66.7	20.0	46.7	15	33.3	4.8	28.6	21	60.0	20.0	20.0	10
Red-bellied Woodpecker	0.0	0.0	0.0	1	0.0	0.0	0.0	1	0.0	0.0	100.0	1
Black-capped Chickadee	66.7	8.3	58.3	12	43.8	6.3	37.5	16	40.0	40.0	20.0	10
Total	58.8	19.6	39.2	51	35.2	14.1	21.1	71	39.5	25.6	34.9	43
Grand Total	56.0	27.0	29.0	100	38.5	20.5	18.0	122	35.8	29.6	34.6	81

[a] Cavity reuse by the same species.
[b] Cavity reuse by other species.
[c] Includes reuse of 2 cavities by fox squirrels.

0.58, $P > 0.05$). Of SCNB cavities, reuse was highest for American Kestrel cavities (66.7%), whereas of the PCNB cavities, chickadee and Red-headed Woodpecker cavities were most frequently reused (66.7%). None of the cavities occupied by Red-bellied Woodpeckers ($n = 1$) or White-breasted Nuthatches ($n = 3$) in 1985 were reused in 1986. Constancy, or reuse of cavities by the same species, was 27% (27/100). For SCNB, it ranged from 0% (Red-bellied Woodpecker cavities) to 56.3% (House Wren cavities; i.e., 9 of 16 old House Wren nest cavities were reused by House Wrens), whereas for PCNB, constancy was highest for Northern Flickers (26.1%). Constancy for SCNB cavities (34.7%) was marginally greater ($t_{98} = 1.71$, $P < 0.10$) than that for PCNB cavities (19.6%). Usability, or the proportion of a given species' cavities used by other species, was lowest for nuthatch (0.0%), Red-bellied Woodpecker (0.0%), and House Wren cavities (6.3%), and was highest for Black-capped Chickadee cavities (58.3%). Usability was significantly greater for PCNB (39.2%) than for SCNB nest cavities (18.4%; $t_{98} = 2.34$, $P < 0.05$). Thus, old cavities of PCNB were more available to other species of cavity-nesting birds, whereas old SCNB cavities tended to be reused by the same species that previously occupied the cavity.

Overall reuse of cavities in 1987 (38.5%; cavities first located in 1985 or 1986) was lower than reuse in 1986 (56%; $t_{220} = 2.61$, $P < 0.01$; Table 1). Reuse in 1987 of cavities found in 1985 (38.8%) and of those found in 1986 (38.1%) was similar ($t_{120} = 0.07$, $P > 0.5$). Similar proportions of SCNB (43.1%) and PCNB (35.2%) cavities were reused ($t_{120} = 0.88$, $P > 0.3$) in 1987. Among SCNB cavities, reuse was highest for House Wren cavities (57.1%), whereas among PCNB cavities, chickadee cavities were most frequently reused (43.8%). Constancy was 20.5% overall (i.e., 25/122 cavities examined were reused by the same species that originally occupied the cavity in 1985 or 1986) and was again highest for House Wren cavities (57.1%). Among PCNB cavities, constancy was again highest for Northern Flicker cavities (24.2%). Constancy for SCNB cavities in 1987 (29.4%) was greater than that for PCNB cavities (14.1%; $t_{120} = 2.05$, $P < 0.05$). Usability was lowest for House Wren, White-breasted Nuthatch, and Red-bellied Woodpecker cavities (0.0%), and highest for Black-capped Chickadee (37.5%) and Red-headed Woodpecker cavities (28.6%). Usability was similar in 1987 for PCNB (21.1%) and SCNB cavities (13.7%; $t_{120} = 1.07$, $P > 0.2$).

Eighty-one of the cavities originally located in 1985 were still intact and monitored in both 1986 and 1987; of these, 29 (35.8%) were reused in either 1986 or 1987, 24 (29.6%) were reused in both years, and 28 (34.6%) were not reused in either year (Table 1). Thus, 53/81 (65.4%) cavities were reused at least once over

TABLE 2. Reuse of 1985 cavities by species (no., [%][a]) in 1986, SPWMA, Colorado.

1985 cavity occupant (*n*)	Species reusing cavities in 1986							
	SCNB				PCNB			
	AMKE[b] (%)	EUST (%)	HOWR (%)	Total SCNB (%)	BCCH (%)	NOFL (%)	RHWO (%)	Total PCNB (%)
AMKE	4	0	1	5	0	0	1	1
(9)	(44.4)	(0.0)	(11.1)	(55.6)	(0.0)	(0.0)	(11.1)	(11.1)
EUST	1	4	3	8	0	2	0	2
(21)	(4.8)	(19.0)	(14.3)	(38.1)	(0.0)	(9.5)	(0.0)	(9.5)
HOWR	0	0	9	9	1	0	0	1
(16)	(0.0)	(0.0)	(56.3)	(56.3)	(6.3)	(0.0)	(0.0)	(6.3)
WBNU	0	0	0	0	0	0	0	0
(3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
BCCH	0	0	7	7	1	0	0	1
(12)	(0.0)	(0.0)	(58.3)	(58.3)	(8.3)	(0.0)	(0.0)	(8.3)
NOFL	1	0	3	4	0	6	0	6
(21[c])	(4.8)	(0.0)	(14.3)	(19.0)	(0.0)	(28.6)	(0.0)	(28.6)
RBWO	0	0	0	0	0	0	0	0
(1)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
RHWO	0	2	4	6	0	1	3	4
(15)	(0.0)	(13.3)	(26.7)	(40.0)	(0.0)	(6.7)	(20.0)	(26.7)
Total	6	6	27	39	2	9	4	15
(98[c])	(6.1)	(6.1)	(27.6)	(39.8)	(2.0)	(9.2)	(4.1)	(15.3)

[a] Percent of 1985 cavities.
[b] Mnemonics for species' names: AMKE = American Kestrel, BCCH = Black-capped Chickadee, EUST = European Starling, HOWR = House Wren, NOFL = Northern Flicker, RHWO = Red-headed Woodpecker, RBWO = Red-bellied Woodpecker, WBNU = White-breasted Nuthatch.
[c] Excluding 2 nests reused by fox squirrels.

a 2-year period. The percentage of cavities reused at least once did not differ between SCNB cavities (65.8%) and PCNB cavities (65.1%; $t_{79} = 0.07$, $P > 0.5$). There was a moderate degree of constancy with 26/81 (32.1%) cavities being reused by the same species as the original occupant in one or both years; 18 cavities were reused by the same species in one of the two years and 8 were reused both years by the same species that occupied it in 1985.

SPECIES' REUSE OF CAVITIES

House Wrens and Northern Flickers reused most of the available cavities in 1986 (Table 2). Of 54 cavities reused by birds, House Wrens reused 27 (50%) and Northern Flickers reused 9 (16.7%). House Wrens reused more than half of all old Black-capped Chickadee and House Wren cavities and 26.7% of old Red-headed Woodpecker cavities. Northern Flickers reused 28.6% of their own old cavities and 9.5% of old European Starling cavities. SCNB reused more of the old 1985 cavities (39.8%) than did PCNB (15.3%).

In 1987, as in 1986, most of the previously occupied cavities were reused by House Wrens (20/122) and by Northern Flickers (14/122; Table 3). House Wrens reused cavities of chickadees (37.5%), wrens (57.1%), and Red-headed Woodpeckers (19.0%). Flickers reused cavities of American Kestrels (16.7%), starlings (13.6%), and flickers (24.2%). Chickadees were most discriminating in the reuse of old cavities in 1987 as they only reused 1 cavity. SCNB used a greater proportion of old cavities (23.8%) than did PCNB (13.9%).

DISCUSSION

The proportion of cavities reused varied substantially from year to year (56% in 1986 and 38.5% in 1987). However, similar proportions of previously occupied SCNB and PCNB cavities were reused in each year, suggesting no difference in desirability between old PCNB and SCNB nests. PCNB reused fewer cavities than SCNB; most PCNB excavate new cavities annually, and are not thought to reuse old cavities frequently. The high reuse of cavities by Northern Flickers compared to other PCNB suggests that flickers may be reusing more cavities than is typical for a primary cavity nester. One possible explanation is that although Northern Flickers may be excavating new cavities each year, these new cavities are being usurped by

TABLE 3. Reuse of 1985 and 1986 cavities by species (no., [%][a]) in 1987, SPWMA, Colorado.

1985–1986 cavity occupant (*n*)	Species reusing cavities in 1987[b]							
	SCNB				PCNB			
	AMKE (%)	EUST (%)	HOWR (%)	Total SCNB (%)	BCCH (%)	NOFL (%)	RHWO (%)	Total PCNB (%)
AMKE	3	0	0	3	0	2	0	2
(12)	(25.0)	(0.0)	(0.0)	(25.0)	(0.0)	(16.7)	(0.0)	(16.7)
EUST	0	3	1	4	0	3	1	4
(22)	(0.0)	(13.6)	(4.5)	(18.2)	(0.0)	(13.6)	(4.5)	(18.2)
HOWR	0	0	8	8	0	0	0	0
(14)	(0.0)	(0.0)	(57.1)	(57.1)	(0.0)	(0.0)	(0.0)	(0.0)
WBNU	0	0	0	0	0	0	0	0
(3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
BCCH	0	0	6	6	1	0	0	1
(16)	(0.0)	(0.0)	(37.5)	(37.5)	(6.3)	(0.0)	(0.0)	(6.3)
NOFL	1	1	1	3	0	8	0	8
(33)	(3.0)	(3.0)	(3.0)	(9.1)	(0.0)	(24.2)	(0.0)	(24.2)
RBWO	0	0	0	0	0	0	0	0
(1)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
RHWO	0	1	4	5	0	1	1	2
(21)	(0.0)	(4.8)	(19.0)	(23.8)	(0.0)	(4.8)	(4.8)	(9.5)
Total	4	5	20	29	1	14	2	17
(122)	(3.3)	(4.1)	(16.4)	(23.8)	(0.8)	(11.5)	(1.6)	(13.9)

[a] Percent of 1985–1986 cavities.
[b] Mnemonics for species' names: AMKE = American Kestrel, BCCH = Black-capped Chickadee, EUST = European Starling, HOWR = House Wren, NOFL = Northern Flicker, RHWO = Red-headed Woodpecker, RBWO = Red-bellied Woodpecker, WBNU = White-breasted Nuthatch.

competitors, forcing flickers to reuse old cavities (Moore 1995). Competition for new cavities may be intense because newly excavated cavities are free of parasites (Short 1979). Starlings are perhaps the most serious competitors for nest sites (Troetschler 1976, Jackson 1977, Ingold 1989, 1994), but other species of woodpeckers also may usurp newly excavated nests (Kilham 1962b, Ligon 1971, Ingold 1994). Conversely, species which reused few old cavities (e.g., Red-headed Woodpecker) presumably excavate and occupy proportionately more new cavities.

SUBSTRATE AND CAVITY RESOURCES

Sedgwick and Knopf (1992) concluded that equilibrium cavity density along the South Platte River on the SPWMA was 238–289 cavities km^{-1} and that 205 cavities km^{-1} were required by SCNB. Based on empirical cavity reuse data (this study), PCNB occupied 15/100 cavities in 1986 and 17/122 in 1987; fox squirrels used another 2 cavities. Thus, 15.3% of the cavities were not available to SCNB and the total number of cavities (t) needed by both SCNB and PCNB may be expressed as:

$$t = 205 + p(t),$$

where 205 is the number of cavities required by SCNB and p is the proportion of the total used by PCNB. This raises the total number of old cavities needed by both SCNB and PCNB to 242 km^{-1} (where p is 0.153), which is above the lower bound of equilibrium cavity density (238 cavities km^{-1}). Hence, cavity availability may be limiting SCNB densities along the South Platte River. Even though numerous (old) cavities remained unoccupied (54% and 61.5%, 1986 and 1987, respectively), similar to other studies of natural populations of hole nesters (Brush 1983, Rendell and Robertson 1989, Waters et al. 1990), the availability of *suitable* cavities may nevertheless be limiting populations of SCNB. Inter- and intraspecific territorial behavior, inadequate food resources, or avoidance of old cavities because of high parasite loads (Rendell and Verbeek 1996) may explain the presence of numerous, unoccupied cavities in populations of cavity-nesting birds.

Because all three major SCNB (wrens, starlings, kestrels) are fairly aggressive in securing cavities (Bent 1948, Balgooyen 1976, Ingold 1989), competition from these species may be a primary cause of cavity reuse by PCNB. Therefore, the reuse of some cavities by PCNB may not effectively limit the cavity resource for

SCNB in this community. However, if cavity reuse by PCNB is due primarily to an inadequate substrate resource (causing old cavities to be at a premium), and not to interference and competition with SCNB, then the *cavity* resource will become the proximate limiting factor for SCNB on the South Platte.

DOES CAVITY REUSE BY PCNB LOWER REPRODUCTIVE OUTPUT?

At some point, when the physical structure of the substrate containing a cavity begins to deteriorate, old cavities become unsuitable for cavity-nesting birds. Occupancy of such cavities may lower reproductive success. Evidence from this study, where n and $n+1$ year-old cavities were reused at the same rate (i.e., 38.8% and 38.1% of 1985- and 1986-found cavities were reused in 1987), suggests that newer holes are not more preferable, and perhaps not intrinsically better than old cavities. However, frequent cavity reuse by flickers, for example, raises concern because of possible phenology shifts. If reuse of old cavities shifts the phenology of the nesting cycle to later in the season (possibly because of repeated usurpation of new cavities), then reproductive output may be diminished. Ingold (1996) found that delayed nesting by flickers as a result of starling competition significantly reduced clutch, nestling, and fledgling numbers. Lowered reproductive output as a result of phenology shifts has been shown for a number of other species, as well, and is often corroborated by lower return rates and increased mortality in late-born young (Perrins 1965, Morton 1992). Red-bellied Woodpeckers unable to avoid starling competition in Mississippi suffered reductions in fecundity, possibly due to lost opportunities for fecundity enhancements from second and third broods (Ingold 1989). To determine whether this is a widespread phenomenon, starling competition and its effects on flicker reproductive success should be examined along the South Platte and elsewhere.

CAVITY REUSE, INTERFERENCE, AND COMPETITION

In two years (Tables 2 and 3), Northern Flickers reused 23 old cavities, whereas Red-headed Woodpeckers reused only 6. This suggests that Red-headed Woodpeckers are using proportionately more new excavations than flickers, and that Red-headed Woodpeckers may be superior competitors for new excavations compared to flickers. The greater similarity in cavity, tree, and habitat characteristics of starlings and flickers compared to starlings and Red-headed Woodpeckers (Sedgwick and Knopf 1990) suggests that starlings are reusing proportionately more old flicker cavities than red-head cavities and/or starlings are more successful in usurping new excavations of flickers than of red-heads. Similarly, in a Red-bellied/Red-headed Woodpecker study (Ingold 1989), starlings appeared to prefer cavities characteristic of Red-bellied Woodpecker (smaller entrances, in substrates with bark, and in limbs angled downward) over those characteristic of Red-headed Woodpecker (larger cavities, more vertical facing, in dead trees without bark).

House Wrens interfere and compete directly and indirectly with other cavity nesters. House Wrens are known to directly compete for cavities during the nest-site selection phase of the breeding cycle (Bent 1948). They also indirectly compete for cavities by making them unusable to other species by depositing large quantities of sticks and other nest materials in cavities. In this study, only 1 of 30 wren cavities in 2 years was reused by another species. High reuse by wrens of old chickadee (58.3% and 37.5%) and Red-headed Woodpecker (26.7% and 19.0%) cavities in 1986 and 1987, respectively (Tables 2, 3), suggests that these species must excavate a higher proportion and reuse a lower proportion of their cavities than species whose cavities are less frequently reused by wrens. This is confirmed by relatively low constancy values for both chickadees and Red-headed Woodpeckers (Table 1).

RELATIVE INFLUENCE OF PCNB

PCNB occurring at the highest densities will have the greatest influence on cavity availability for SCNB, assuming cavity excavation rates are equivalent. On the SPWMA, Black-capped Chickadee cavities should be most numerous because population densities of chickadees are about four times greater than those of Red-headed Woodpeckers and Northern Flickers (Sedgwick and Knopf 1986). Chickadee cavities have a high percentage usability as well (Table 1). However, because of the small cavity entrance diameter of chickadee cavities, old chickadee cavities were reused only by House Wrens (7/12 and 6/16 chickadee cavities reused in 2 years by

wrens; Tables 2 and 3). The densities of flickers and Red-headed Woodpeckers are about equal on the SPWMA, but Red-headed Woodpecker cavities have greater usability than flicker cavities, at least in part because Red-headed Woodpeckers infrequently reuse their own cavities (Table 1). Flicker cavities, however, provided nest substrate for a somewhat greater array of species (kestrel, wren, starling, fox squirrel) than did Red-headed Woodpecker cavities (wren, starling, flicker). In addition, if frequent cavity usurpation of flicker nests results in multiple cavity excavations, then flickers may provide the majority of large cavities along the South Platte River for later use by SCNB.

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